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ESTIMATING THE CONTRIBUTION OF MUSCLES TO JOINT TORQUE BASED ON MOTOR-UNIT ACTIVITY

M. Theeuwes, C. C. A. M. Gielen and B. M. van Bolhuis

Department of Medical Physics and Biophysics, University of Nijmegen, Geert Grooteplein Noord 21,
 NL 6525 EZ Nijmegen, The Netherlands

Abstract—Because most joints in the human arm are crossed by a number of muscles which exceeds the number of degrees of freedom for those joints, the motor system can use a variety of muscle activation patterns for the same torque in each joint. We have developed a model to estimate the contribution of individual muscles to the total torque in a joint based on intramuscular EMG recordings. EMG activity recorded with surface electrodes may be contaminated with cross-talk from other muscles. Moreover, it may not be representative for the activation of a muscle when there are several subpopulations of motor units in the muscle. We derive a relation between the recruitment threshold of a motor unit in a subpopulation for force in various directions and the relative contribution by that subpopulation to joint torque. A set of linear equations can then be constructed which relates the contribution of each subpopulation (and therefore of each muscle) to the total joint torque. If the activation of individual subpopulations is modulated differently for forces in various directions, the relative contribution of the individual subpopulations to the total joint torque can be estimated. Copyright © 1996 Elsevier Science Ltd.

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INTRODUCTION

The force exerted at the end effector of a limb is the result of the torques in each of its joints. Since in general more than one single muscle is acting across a joint, it is hard to determine the individual contribution of each of the muscles to joint torque. However, there are several reasons why it is important to know the contribution of each single muscle to total joint torque. For example, there are various theories on the role of mono- and bi-articular muscles (see e.g. van Ingen Schenau, 1989; Jacobs and van Ingen Schenau, 1992) and about the role of muscles with parallel oriented muscle fibers and of muscles with a pennate structure (Otten, 1988; Woittiez *et al.*, 1984). Knowledge of the contribution of individual muscles to joint torque in natural movements will make it possible to test these hypotheses and will contribute to a better understanding of muscle coordination in mechanically redundant limbs.

In addition to these reasons a quantitative method for this purpose would also be highly desirable since recent studies have shown that the relative activation of muscles for a particular joint torque is not constant, but dependent on the motor task (see e.g. Tax *et al.*, 1989, 1990a,b). Quantitative information about the task-dependent contribution of muscles to joint torque may reveal more information on the particular role of mono- and bi-articular muscles (see e.g. Gielen and van Ingen Schenau, 1992; van Ingen Schenau, 1989).

Usually, surface EMG recordings have been used to estimate the activation of various muscles and to deter-

mine their role in various movements. However, the absolute value of EMG activity depends on a variety of factors such as the position of the surface electrodes relative to the active muscle fibres, the thickness of subcutaneous fat layers, blood vessels, etc. Therefore, EMG activity by itself can only provide a qualitative, not a quantitative measure of the contribution of a muscle to joint torque. Moreover, the EMG-force relationship is not fixed but task-dependent such that EMG is not a unique measure for muscle force (see e.g. Miller *et al.*, 1992; Theeuwes *et al.*, 1994b).

In the past several studies have tried to estimate the relative contribution of muscles to joint torque. Usually, several additional assumptions had to be made. For example, Jørgenson and Bankov (1971) based their predictions on the physiological cross-sectional area of muscles. Since each muscle may have several subpopulations of motor units, each with a different activation, only a limited set of motor units is active at the same time for force in a particular direction (see e.g. ter Haar Romeny *et al.*, 1984; van Zuylen *et al.*, 1988). Therefore, the physiological cross-sectional area of a muscle is not representative for the area of muscle which is involved in the production of force in a particular direction. More in general, it is very hard to estimate the reliability of results from approaches which are based on assumptions on muscle physiology and on biomechanical properties (see e.g. Challis and Kerwin, 1994).

Other approaches (e.g. Hatze, 1976; Pedotti *et al.*, 1978; Penrod *et al.*, 1974; Zajac *et al.*, 1984) have used optimization techniques which minimized or maximized some objective function. However, for many movements it is not easy to identify an objective criterion for minimization or maximization and, if one is found, it is still an open question whether the central nervous system uses

the optimization of that particular criterion for the co-ordination of muscles. Other approaches have estimated the contribution of a muscle to joint torque by relating the EMG activity of a set of muscles to joint torque. When the EMG activity of the muscles is modulated independently, the contribution of each muscle can be calculated when the set of independent equations is at least equal to the number of muscles involved (see e.g. An *et al.*, 1983; Cnockaert *et al.*, 1975).

Although this method seems to work well for relatively simple joints with a limited set of muscles acting across the joint (see e.g. An *et al.*, 1983; Buchanan *et al.*, 1993), it failed for the highly redundant muscle system of the human elbow (see Buchanan, 1986). It is not clear yet, whether this is due to the inevitable cross talk from other muscles or due to other noise in the measurements.

The aim of this paper is to present a method to determine the contribution of a muscle to joint torque, when several muscles act across that joint, based on motor-unit data. The advantage of single motor-unit activity above surface EMG recordings is that crosstalk from other muscles, a well-known problem with surface EMG which may corrupt estimates on the contribution of muscles to joint torque, is avoided. In a previous paper (Theeuwen *et al.*, 1994a) we have shown how the recruitment threshold of a motor-unit from a particular subpopulation of motor units for forces at the limb in various directions can be related to variations of torque contributed by that subpopulation. However, the absolute value of the torque contribution could not be estimated in that study. From there on our approach is basically similar to that described by Cnockaert *et al.* (1975) since we also make the assumption that there exists a unique scaling factor relating force generated by a specific subpopulation of motor units to joint torque contributed by that subpopulation in a particular motor task (e.g. for isometric or for isotonic contractions). When the recruitment behaviour of motor-unit (sub) populations is available in force conditions in which the relative contribution by the muscles varies, one obtains an independent set of equations, which allows the determination of the contribution of each muscle or subpopulation. This procedure allows an accurate estimation of the contribution of the various groups of motor-unit subpopulations to joint torque.

THEORY

In a previous paper (Theeuwen *et al.*, 1994a) we have explained how variations in recruitment threshold of motor units for force in various directions can be related to variations in the amount of EMG activity recorded with surface electrodes. The same line of reasoning gives the relation between recruitment thresholds and the relative contribution to torque by that subpopulation for force in various directions.

First we assume that motor units of one subpopulation are recruited in an orderly manner according to the size principle described by Henneman (1981). This means that

all motor units in that subpopulation have a recruitment behaviour which is modulated in the same way for forces in various directions. If for forces in a particular direction the recruitment threshold of one motor unit is raised by a certain factor, this is assumed to be representative for the behaviour of all other motor units in the same subpopulation. This is confirmed by the finding that recruitment thresholds of motor units for torques in several directions lie on straight parallel lines as reported by ter Haar Romeny *et al.* (1982), by van Zuylen *et al.* (1988) and by Theeuwen *et al.* (1994a,b).

Secondly, we assume that a line of recruitment thresholds represents a line of torques where the activation and torque contribution of the subpopulation of motor units is constant.

With these assumptions the precise contribution of a muscle to joint torque can be determined in the following way. It has been shown before that, when the direction of the external torque changes, the relative activation of muscles (and therefore also their relative contribution to torque in joint j) will change (see e.g. Buchanan *et al.*, 1986; Miller *et al.*, 1992; Theeuwen *et al.*, 1994a) proportionally to the innerproduct of joint torque \mathbf{T}_j and the normal $\mathbf{T}_{\text{nor},m}$ to the recruitment line of motor units in subpopulation m

$$\mathbf{T}_{m,j} = \begin{cases} \mathbf{C}_{m,j} (\mathbf{T}_j \cdot \mathbf{T}_{\text{nor},m}) & \text{for } (\mathbf{T}_j \cdot \mathbf{T}_{\text{nor},m}) \geq 0, \\ 0 & \text{for } (\mathbf{T}_j \cdot \mathbf{T}_{\text{nor},m}) \leq 0. \end{cases} \quad (1)$$

In this equation $\mathbf{T}_{m,j}$ represents the contribution by the (sub)population motor units m to torque in joint j . At a given activation level of the muscle $\mathbf{T}_{\text{nor},m}$ represents the recruitment threshold of the motor unit, which is just recruited at that activation level. Obviously, for larger activation levels, more motor units are recruited and $\mathbf{T}_{\text{nor},m}$ increases in size, not in direction. The direction of $\mathbf{C}_{m,j}$ (i.e. $\mathbf{C}_{m,j}/\|\mathbf{C}_{m,j}\|$) is anatomically defined. For *m. biceps, caput longum*, for example, the component of \mathbf{C} in flexion direction will be about 5 times larger than that in supination direction due to the fact, that the lever arm for flexion is about 5 times larger than that for supination (see ter Haar Romeny *et al.*, 1984). The magnitude of $\mathbf{C}_{m,j}$ is a proportionality constant which has to be determined in order to estimate $\mathbf{T}_{m,j}$. Obviously, it is different for different joint angles.

Since the sum of the contributions of all muscles to total joint torque is uniquely defined

$$\sum_{m=1}^M \mathbf{T}_{m,j} = \mathbf{T}_j = \mathbf{r}_j \times \mathbf{F}_e, \quad (2)$$

with \mathbf{r}_j the lever arm relative to joint j , then a set of linear equations relating the contribution by each muscle to total joint torque can be constructed for various directions of external force \mathbf{F}_e . By varying the direction ϕ of the externally required force \mathbf{F}_e the relative contribution from the active muscles across a joint j are modulated independently (see e.g. Buchanan *et al.*, 1986; Miller *et al.*, 1992; Theeuwen *et al.*, 1994a; van Zuylen *et al.*, 1988). When N different directions ϕ_i are tested, this allows the construction of a set of N linear equations from which the

Coefficients $\|C_{m,j}\|$ can be solved:

$$\sum_{m=1}^M \|C_{m,j}\| \cdot \frac{C_{m,j}}{\|C_{m,j}\|} (T_j(\phi_i) \cdot T_{nor,m}) = T_j(\phi_i),$$

$$i \in \{1, 2, \dots, N\}. \quad (3)$$

If these equations are linearly independent, which is the case if the relative recruitment thresholds of motor units in various muscles vary in a different way for various directions of force F_e , this set can be solved and the proportionality constants $\|C_{m,j}\|$ between muscle torque and externally required joint torque can be obtained for each single muscle. If N exceeds the number M of muscles or motor-unit subpopulations, this system is overdetermined and the set of equations will not be linearly independent. This set of equations can be considered as a matrix equation with the matrix coefficients $C_{m,j}/\|C_{m,j}\| (T_j(\phi_i) \cdot T_{nor,m})$ and the unknown variables $\|C_{m,j}\|$. A singular value decomposition, for example, can then be used to investigate how many independent equations exist in the set. It should be notified, that a solution for the coefficients $C_{m,j}$ is valid only for one single joint angle, since these coefficients depend on the force-length relationship and on the muscle mechanical advantage.

DATA

The motor-unit data were taken from van Zuylen *et al.* (1988). In this study averaged data are presented for recruitment thresholds of motor units in various subpopulations in m. biceps brachii, m. brachioradialis, m. brachialis, m. triceps (lateral head, medial head and long head), m. supinator, and pronator teres for isometric contractions. For m. pronator quadratus, the pure antagonist of m. supinator, no data were available. For this muscle, we simulated data based on the data of its antagonist m. supinator. In the discussion it will be argued, that based on biomechanical considerations any other type of behaviour for the motor units in m. pronator quadratus is not plausible. The effect of small variations in the precise, quantitative behaviour of these motor units appears to be small (see Results and Discussion).

RESULTS

An extensive report on the recruitment behaviour of motor units in human elbow muscles for various combinations of isometric torque in flexion/extension and pronation/supination directions was given by van Zuylen *et al.* (1988). These authors reported on subpopulations of motor units within the same muscle with a distinctively different recruitment behaviour despite the fact that all motor units have the same mechanical effect because they share the same tendons (see ter Haar Romeny *et al.*, 1984). These subpopulations have to be handled as separate muscle units. Based on the paper by van Zuylen *et al.* (1988) we took all 13 subpopulations of motor units into account which were reported in that study. The recruit-

ment threshold of motor units in these subpopulations as a function of the combination of flexion/extension (F/E) torque and supination/pronation (S/P) torque is summarized in Fig. 1 and can also be found in van Zuylen *et al.* (1988).

Because no data were available for m. pronator quadratus, we assumed a recruitment behaviour for its motor units opposite to that of its antagonist m. supinator. The consequences of this choice will be discussed later.

For all subpopulations of motor units shown in Fig. 1 we calculated the unscaled muscle activation $(C_{m,j}/\|C_{m,j}\|)(T_j \cdot T_{nor})$ for combinations of torques in flexion/extension and supination/pronation direction. Figure 2 shows the torque contribution of the subpopulations of motor units with a recruitment behaviour illustrated in Fig. 1 for various combinations of flexion/extension-torques and supination/pronation-torques. If the recruitment thresholds fall along a straight line (such as in Fig. 1A) the torque contribution is given by a circle (see Theeuwes *et al.*, 1994a). If the recruitment behaviour of a motor unit is described by a concatenation of different line segments, as for m. biceps subpopulation 2 (Fig. 1C), a transformation can be found for each of the line segments. With the requirement of continuity the concatenation of circle segments in Fig. 2C can be derived.

Only the scaling constants $\|C_{m,j}\|$ representing the relative contribution of these subpopulations to the total torque T_j have to be determined. As described in the theory section, a matrix equation [equation (3)] can be constructed for these data to calculate the scaling constants.

Some muscles generate torques which have components both for flexion/extension and for supination/pronation. The ratio of the flexion/extension and supination/pronation torque components is defined by the anatomical lever arms of the muscles (see e.g. Fick, 1911; Lohman, 1976; Sobotta and Becher, 1972). This determines $C_{m,j}/\|C_{m,j}\|$. For each direction both the required flexion/extension torque and the supination/pronation torque have to be satisfied. This results in two equations per direction with just one unknown scaling parameter $\|C_{m,j}\|$ per muscle or subpopulation of motor units.

A singular value decomposition has been used to find the eigenvalues and eigenvectors of the matrix with coefficients $(C_{m,j}/\|C_{m,j}\|)(T_j(\phi_i) \cdot T_{nor,m})$ obtained with equation (3) in order to find the scaling constants $\|C_{m,j}\|$ necessary to relate the recruitment behaviour of individual muscles or of subpopulations of motor units to the total joint torque. The singular value decomposition revealed that $(M - 3)$ eigenvalues differed significantly from zero. This means that there exists a three-dimensional solution space instead of just one single unique solution. One dimension of this solution space comes from the three subpopulations in m. biceps. The activation pattern of subpopulation 3 of this muscle (see Fig. 1C) can be constructed by a linear combination of activation patterns of subpopulations 1 and 2 (see Fig. 1A and B). The recruitment behaviour of subpopulation 3 is the same as that for subpopulation 1 in the (F/P)-quadrant,

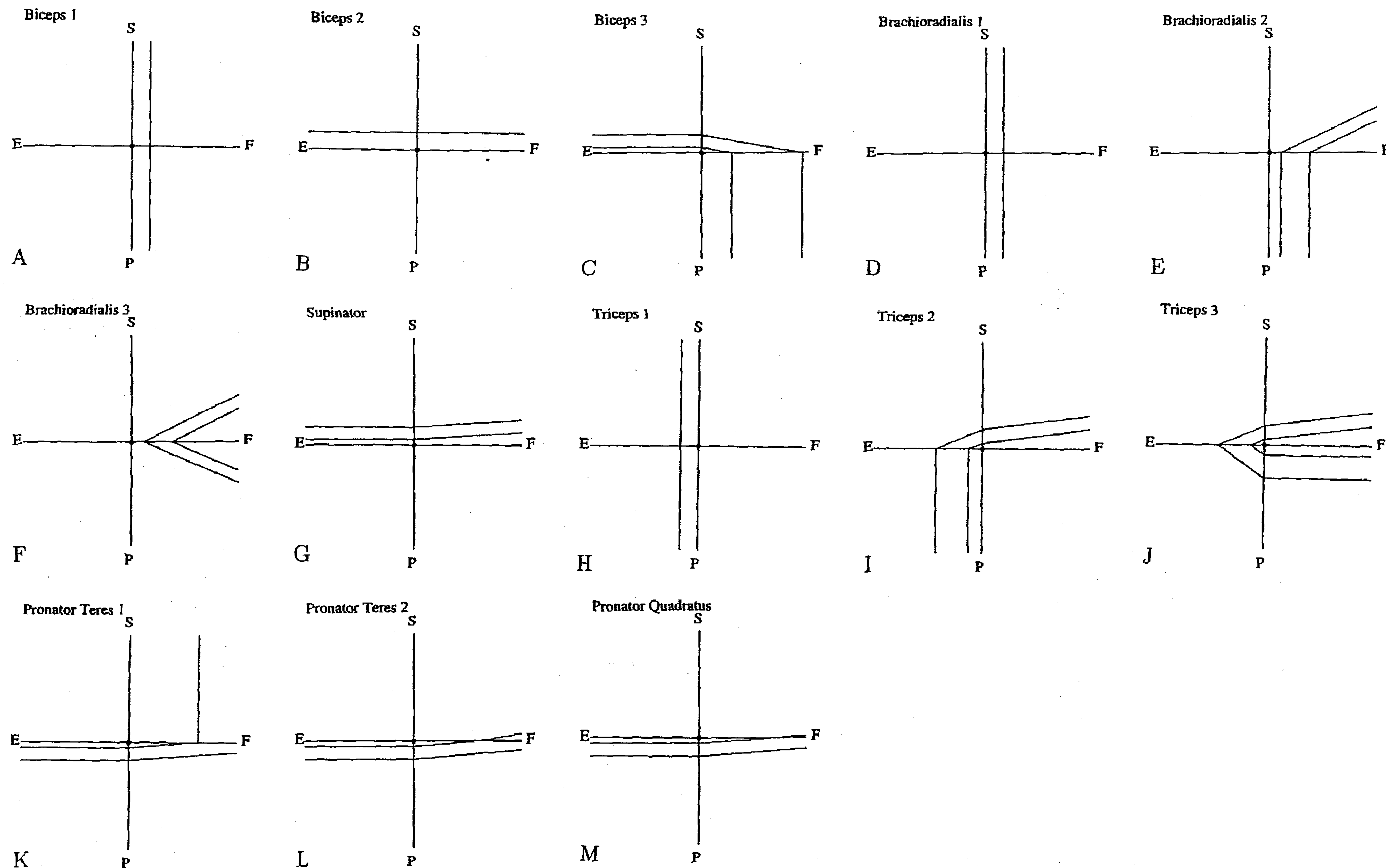


Fig. 1. The behaviour of the recruitment thresholds as a function of the combination of flexion (F), supination (S), extension (E) and pronation (P) for several elbow muscles and subpopulations of motor units within a muscle. In the panels are shown m. biceps subpopulation 1 (A), m. biceps subpopulation 2 (B), m. biceps subpopulation 3 (C), m. brachioradialis subpopulation 1 (D), m. brachioradialis subpopulation 2 (E), m. brachioradialis subpopulation 3 (F), m. supinator (G), m. triceps subpopulation 1 (H), m. triceps subpopulation 2 (I), m. triceps subpopulation 3 (J), m. pronator teres subpopulation 1 (K), m. pronator teres subpopulation 2 (L) and m. pronator quadratus (M). These data are taken from van Zuylen *et al.* (1988).

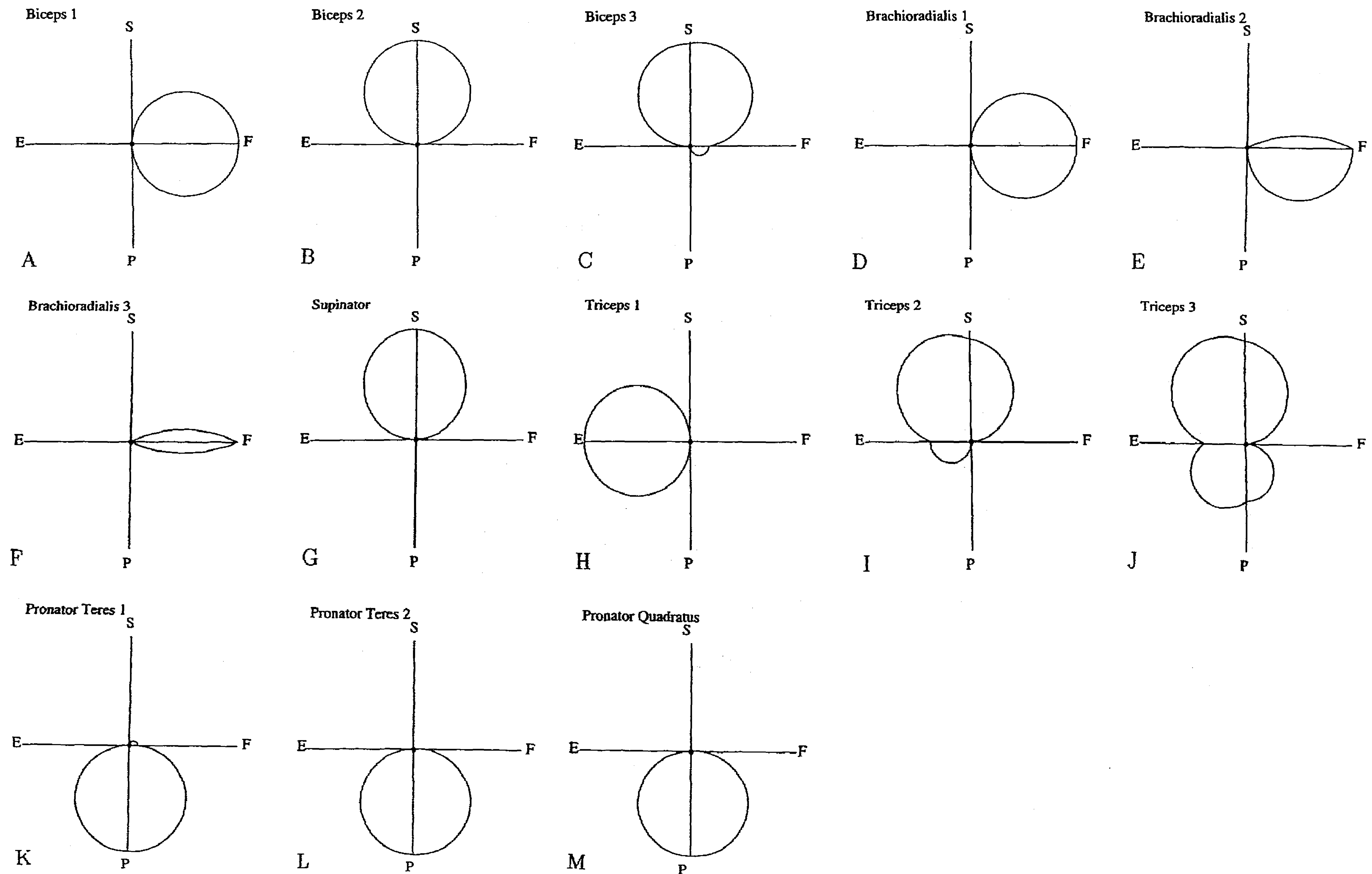


Fig. 2. The result of the estimation procedure to estimate the torque contribution of various subpopulations of motor units as a function of the combination of flexion (F), supination (S), extension (E) and pronation (P). The recruitment thresholds of these motor-units are shown in Fig. 1. In the panels are shown m. biceps subpopulation 1 (A), m. biceps subpopulation 2 (B), m. biceps subpopulation 3 (C), m. brachioradialis subpopulation 1 (D), m. brachioradialis subpopulation 2 (E), m. brachioradialis subpopulation 3 (F), m. supinator (G), m. triceps subpopulation 1 (H), m. triceps subpopulation 2 (I), m. triceps subpopulation 3 (J), m. pronator teres subpopulation 1 (K), m. pronator teres subpopulation 2 (L) and m. pronator quadratus (M).

the same as that for subpopulation 2 in the (S/E)-quadrant and the same as the combination of these subpopulations in the (F/S)-quadrant.

The second dimension of this solution space comes from the fact that the contribution from *m. supinator* can be exchanged by a contribution from *m. biceps* subpopulation 2 and 3 when supination torques are involved. Therefore, two subpopulations from *m. biceps* can be active when a torque with a component in supination direction is present. Because *m. biceps* has a mechanical contribution to flexion torque, this contribution to flexion torque, which is generated during supination, has to be canceled for pure supination torques and for combined supination and extension torques. This can be done by activating the subpopulations 2 and 3 in *m. triceps* (see Fig. 1I and 1J). For combinations of extension and supination torque, the activity of subpopulation 1 of *m. triceps*, which is activated for extension torques only (Fig. 1H), is then also determined because it has to contribute the remaining extension torque which is not provided by subpopulations 2 and 3.

The third dimension of this solution space comes from motor units labeled 'm. pronator teres 2' for pronation torques. In addition to *m. pronator quadratus* this muscle can contribute mechanically to torque in pronation direction. However, since *m. pronator teres* has also a mechanical component in flexion direction, the undesired flexion torques, when a pure pronation torque has to be generated, can be compensated by activation of *m. triceps* subpopulation 3, which is the only subpopulation of *m. triceps* which can be activated in the flexion/pronation-quadrant. The activation of *m. pronator teres* relative to the activation of *m. pronator quadratus* determines the relative contribution of the subpopulations 2 and 3 of *m. triceps*.

Given these three degrees of freedom in the solution space, the activation of the other pools of motor units is uniquely determined. The use of *m. pronator teres* subpopulation 2 determines the ratio between the activation of *m. triceps* subpopulation 2 and 3. Only subpopulation 3 can compensate the flexion torque of *m. pronator teres*. *M. pronator quadratus* generates the remainder of the pronation torque.

For torques with a supination component the activation of the subpopulations 1 and 3 in *m. biceps* is determined by the slope of the recruitment lines for *m. supinator* in the flexion/supination-quadrant. For joint torques with mainly a flexion component, activation of subpopulations 1 and 3 leads automatically to a contribution by these muscles to supination torques as well. Because the total joint torque already has a small supination component, which is now mainly generated by *m. biceps*, the contribution from *m. supinator* has to be small. The slope of the recruitment line for *m. supinator* determines to what extent the relative contribution by *m. supinator* to the total supination torque in the elbow changes for variations in flexion torque superimposed on a supination torque. For these joint torques, the relative contribution from *m. biceps* sub-

populations 1 and 2 to the supination torque and hence to the flexion torque in the elbow can increase.

Similarly, the maximal activity of motor units in subpopulations 1 and 3 of *m. biceps* is also determined by the slope of recruitment lines of motor units in *m. pronator quadratus* in the (F/P)-quadrant. Here *m. biceps* generates a mechanical contribution to supination torque when it is activated for flexion torques. This undesired supination torque has to be compensated for by *m. pronator quadratus*, which gives a lower recruitment threshold for pronation when flexion torques are involved. The flexion torque can be provided by *m. biceps*, *m. pronator teres* and *m. brachioradialis*. Given the contribution from *m. biceps* and *m. pronator teres*, the flexion torque which is not generated by these muscles must be generated by *m. brachioradialis*.

Without additional constraints, except for the requirement that all muscles must have an activation which is not negative, the three degrees of freedom in the solution space cannot be removed and within the solution space each solution is equally probable. Therefore, only ranges of relative contributions can be given. The ranges of relative contributions of the individual muscles to torques in pure flexion, supination, extension and pronation torques are given in Table 1. The main contribution (57–80%) to a pure flexion torque comes from motor units from subpopulation 1 in *m. brachioradialis* and *m. brachialis*. Subpopulation 2 in these muscles provides less than 4% of the total torque. Subpopulation 3 is not used at all. The subpopulations 1 and 3 in *m. biceps brachii* contribute 20–43% to flexion torque. (Subpopulation 2 is not activated for a torque without a supination component.) Subpopulation 2 in *m. pronator teres* is predicted to provide at most 2% of the flexion torque. The subpopulation 1 in *m. pronator teres* is not used at all. Supination torque is mainly provided by *m. supinator* (87–100%) and for a small part by *m. biceps* subpopulations 2 and 3. *M. pronator quadratus* generates 88–100% of the pronation torque. *M. pronator teres 2* generates no more than 12% of the pronation torque. Because the maximal activation of *m. triceps* subpopulations 2 and 3 is determined by the activation of *pronator teres 2* and by the activation of *m. biceps* (subpopulations 2 and 3), the contributions from these subpopulations to extension torque is limited to at most 34%. Subpopulation 1 in *m. triceps* generates the remaining 66–100% of the extension torque.

The standard deviation of the results in Table 1 depends both on the accuracy of the data presented by van Zuylen *et al.* (1988) as well as on the accuracy on the data on the relative lever arms of the bi-articular muscles, like *m. biceps brachii* and *m. pronator teres*. Numerical simulations showed that given the standard deviation in the data by van Zuylen *et al.* (1988), the standard deviation in the data shown in Table 1 is less or equal than 10% of the value presented in Table 1. If the results in Table 1 are used to predict joint torques, the error in the estimates was about 5% which indicates that the results of our approach may be helpful in estimating both muscle forces and joint torques.

Table 1. The ranges for the relative contributions of individual muscles and subpopulations of motor units within a muscle to the total elbow torque for pure flexion (F), supination (S), extension (E) and pronation (P). These estimates are based on recruitment data reported in van Zuylen *et al.* (1988)

	F	S	E	P
M. biceps 1 + 3	20–43%	—		
M. biceps 2 + 3	—	0–13%		
M. brachioradialis 1 + 2	57–80%			
M. brachioradialis 3	—			
M. supinator		87–100%		
M. triceps 1			66–100%	
M. triceps 2 + 3			0–34%	
M. pronator teres 1	—			—
M. pronator teres 2	0–2%			0–12%
M. pronator quadratus				88–100%

DISCUSSION

In order to understand the coordination of muscle activation patterns several studies have proposed constraints, which give rise to a reduction of degrees of freedom (see Dul *et al.* 1984; Gielen and van Ingen Schenau, 1992; Yeo 1976). In this study we have chosen another approach in which we started from the experimental data on motor-unit recruitment behaviour. Based on these data, we have tried to estimate the relative contribution of muscles to joint torque.

Several attempts to estimate the relative contribution of muscles to the total torque in a joint have been reported, see e.g. Cnockaert *et al.* (1975), Jørgenson and Bankov (1971) and van Zuylen *et al.* (1988). Jørgenson and Bankov (1971) estimated the relative contribution based on the physiological cross-sectional area of the muscles. Because of the existence of multiple subpopulations of motor units within one muscle with different activation patterns (see e.g. van Zuylen *et al.*, 1988), the physiological cross-sectional area may not be a good criterion for the estimation of the relative contribution from individual muscles to total joint torque.

Our approach is basically similar to that proposed by Cnockaert *et al.* (1975), who based their estimates on a linear relationship between the EMG activity from m. biceps and m. brachioradialis and elbow torque. The EMG activity of these muscles was measured under three conditions: flexion, flexion with supination and flexion with pronation. From these three conditions they constructed a matrix equation similarly to ours. Our method for estimating the relative contribution of individual muscles to the total joint torque using motor-unit data has advantages above previous methods. For example, it is difficult to measure EMG accurately and without crosstalk. Moreover, it contributes to the reduction of the effect of noise to construct an overdetermined matrix equation. The estimation by Cnockaert *et al.* for the relative contributions to the total flexion torque, which was based on the necessary (not overdetermined) number

of data to solve the matrix equation, could differ by more than 40% due to variability in noise. These variations are substantially larger than the 10% standard deviation which we typically find. Also the method proposed by Cnockaert *et al.* (1975) for estimating the relative contribution from individual muscles to the total torque in a joint based on surface EMG, is limited in use if multiple subpopulations of motor units are active, because then the same amount of EMG, even without noise, can correspond to different torques. To correctly incorporate the activity from these subpopulations, intramuscular EMG activity has to be measured.

A comparison of the results obtained in this study with predictions of various models argues against some of these models. For example, the principle of minimum total muscle force (Yeo, 1976) can be eliminated as a principle to reduce the number of degrees of freedom. If such a model were to be used, then m. biceps should not be used for supination and flexion torques, since these torques require the activation of an extensor or pronator muscle, respectively, in order to compensate for the 'undesired' flexion and supination components, respectively, of m. biceps. The activation of these additional muscles increases total muscle torque. Moreover, the principle of minimum fatigue would predict that the activation of muscles with a similar fibre-type composition is the same. Based on the scarce data on the distribution of type I and type II fibres in elbow flexor muscles, we expect that the relative contribution of the flexor muscles is more or less proportional to the product of the muscle cross-sectional area and the mechanical advantage of each muscle. The relative contributions for m. biceps and for m. supinator to supination in Table 1 are not in agreement with such a principle. The results of Bouisset *et al.* (1976) that m. brachialis is the flexor 'par excellence' also argues against this hypothesis. The data in this paper do not allow yet to explain the constraints which underlie the activation of muscles in flexion/extension and supination/pronation direction. Analysis of similar data in more experimental conditions will be necessary to achieve this purpose.

Estimates of the relative contributions from individual muscles or subpopulations of muscles based on intramuscular EMG activity have been reported by van Zuylen *et al.* (1988). They assumed that the number of recordings of motor units belonging to one of the subpopulations in m. biceps and triceps brachii from which they obtained recordings, was a reliable estimate for the distribution of muscle fibres over the individual subpopulations. Furthermore, they assumed that the contribution of subpopulations is proportional to the number of muscle fibres in each of the subpopulations. The first assumption may be heavily biased because recordings from motor units near the boundaries of the muscle, where two subpopulations of motor units are located (see ter Haar Romeny *et al.*, 1984), are difficult to obtain. However, the estimate of 38% made by van Zuylen *et al.* for the contribution of m. biceps to flexion torque falls well in the range for the estimated contribution of m. biceps which is predicted by our method (see Table 1).

The recruitment behaviour of m. pronator quadratus has not been measured directly. From this deep muscle no surface EMG recordings can be obtained. Intramuscular recordings are difficult to obtain because this muscle is thin. Because scratching of the bone underneath this muscle with a needle, while inserting the intramuscular electrodes, would cause some discomfort to the subject, no attempts have been made to record from this muscle. Therefore, we made an initial guess of the recruitment behaviour for m. pronator quadratus based on the behaviour of its antagonist m. supinator. For several variations on this initial guess, we constructed a matrix equation as described in the Theory and Results sections to make estimations of the relative contributions of individual muscles and subpopulations of motor units to the joint torque. For the recruitment behaviour shown in Fig. 2M the discrepancy between the externally required elbow torque and the sum of the individual contributions from muscles and subpopulations of motor units was virtually absent. Any deviations from this behaviour resulted in an increased discrepancy. This suggests that our assumption about the recruitment behaviour of motor units in m. pronator quadratus was quite plausible.

The methods outlined above cannot separate the contributions from subpopulations or muscles with the same recruitment behaviour and with the same activation pattern unless they have a distinctly different mechanical effect. For m. brachioradialis and m. brachialis the relative contributions from the individual muscles cannot be distinguished, because they show similar activation patterns (see e.g. Jongen *et al.*, 1989). Only the combined contribution from these muscles could be estimated.

Finally, it should be mentioned that the results obtained in this study are valid only for isometric contractions. For other motor tasks, such as shortening or lengthening contractions, the relative activation of muscles is different (see Theeuwen *et al.*, 1994b) and, as a consequence, the relative contribution of muscles to torque in these motor tasks will be different too. If data on motor-unit recruitment behaviour are available for these conditions, the relative contribution of the subpopulation can be estimated in a similar way as described above for the isometric condition. Moreover, the assumptions on which our method for estimating the relative contribution of muscles is based, is not applicable for large joint torques, when rate modulation becomes the major mechanism for force gradation.

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REFERENCES

- An, K. N., Cooney, W. P., Chao, E. Y., Askew, L. J. and Daube, J. R. (1983) Determination of forces in extensor pollicis longus and flexor pollicis longus of the thumb. *J. Appl. Physiol.* **54**, 714–719.
- Bouisset, S., Lestienne, F. and Maton, B. (1976) Relative work of main agonists in elbow flexion. International Series on Biomechanics, Vol. Ia. *Proc. 5th Intn. Cong. on Biomech.* (Edited by Komi, P. V.), University Park Press, Jyväskylä, Finland.
- Buchanan, T. S. (1986) A biomechanical analysis of the neural control of muscles about the human elbow joint during isometric tasks. Ph.D. thesis, Northwestern University, Evanston, IL.
- Buchanan, T. S., Almdale, D. P. J., Lewis, J. L. and Rymer, W. Z. (1986) Characteristics of synergic relations during isometric contractions of human elbow muscles. *J. Neurophysiol.* **56**, 1225–1241.
- Buchanan, T. S., Moniz, M. J., Dewald, J. P. A. and Rymer, W. Z. (1993) Estimation of muscle forces about the wrist joint during isometric tasks using an EMG coefficient method. *J. Biomechanics*. **26**, 547–560.
- Challis, J. H. and Kerwin, D. G. (1994) Determining individual muscle forces during maximal activity: model development, parameter determination, and validation. *Hum. Movt Sci.* **13**, 29–61.
- Cnockaert, J. C., Lensel, G. and Pertuzon, E. (1975) Relative contribution of individual muscles to the isometric contraction of a muscle group. *J. Biomechanics* **8**, 191–197.
- Dul, J., Johnson, J. E., Shiavi, R. and Townsend, M. A. (1984) Muscular synergism. II. A minimum fatigue criterion for load sharing between synergistic muscles. *J. Biomechanics* **17**, 675–684.
- Fick, R. (1911) Handbuch der Anatomie und Mechanik der Gelenke. III. Teil: Spezielle Gelenk- und Muskelmechanik. Jena Verlag von Gustaf Fischer; pp. 274–332.
- Gielen, C. C. A. M. and van Ingen Schenau, G. J. (1992) The constrained control of force and position in multi-link manipulators. *IEEE Trans. Systems Man and Cybernet.* **22**, 1214–1219.
- ter Haar Romeny, B. M., Denier van der Gon, J. J. and Gielen, C. C. A. M. (1982) Changes in recruitment order of motor units in the human biceps muscle. *Exp Neurology* **78**, 360–368.
- ter Haar Romeny, B. M., Denier van der Gon, J. J. and Gielen, C. C. A. M. (1984) Relation of the location of a motor unit in human biceps muscle and its critical firing levels for different tasks. *Exp Neurology* **85**, 631–650.
- Hatze, H. (1976) The complete optimization of human motion. *Math. Biosci.* **28**, 99–135.
- Henneman, E. (1981) Recruitment of motoneurons: the size principle. In *Motor Unit Types, Recruitment, and Plasticity in Health and Disease, Progress in Clinical Neurophysiology*, Vol. 9, pp. 26–60. Karger, Basel.
- van Ingen Schenau, G. J. (1989) From rotation to translation: constraints on multi-joint movements and the unique action of bi-articular muscles. *Hum Movt Sci.* **8**, 865–882.
- Jacobs, R. and van Ingen Schenau, G. J. (1992) Control of an external force in leg extensions in humans. *J. Physiol.* **457**, 611–626.
- Jongen, H. A. H., Denier van der Gon, J. J. and Gielen, C. C. A. M. (1989) Activation of human arm muscles during flexion/extension and supination/pronation tasks: a theory on muscle coordination. *Biol. Cybern.* **61**, 1–9.
- Jørgenson, K. and Bankov, S. (1971) Maximum strength of elbow flexors with pronated and supinated forearm. In *Medicine and Sport 6: Biomechanics*, Vol. II, pp. 174–180. Karger, Basel.
- Lohman, A. H. M. (1976) Vorm en beweging: leerboek van de mens. Deel II: platen. Bohn, Scheltema en Hoeksema, Utrecht.
- Miller, L. E., Gielen, C. C. A. M., Theeuwen, M. and Doorenbosch, D. (1992) The activation of mono- and biarticular muscles in multijoint movements. In *Control of Arm Movement in Space. Neurophysiological and Computational Approaches* (Edited by Caminiti, R., Johnson, P.B. and Burnod, Y.), pp. 1–15. Springer, Heidelberg.
- Otten, B. (1988) Concepts and models of functional architecture in skeletal muscle. *Exercise Sport Sci. Rev.* **16**, 89–137.

- Pedotti, A., Krishnan, V. V. and Stark, L. (1978) Optimization of muscle force sequencing in human locomotion. *Math. Biosci.* **38**, 57–76.
- Penrod, D. D., Davy, D. T. and Singh, D. P. (1974) An optimization approach to tendon force analysis. *J. Biomechanics* **7**, 123–129.
- Sobotta, J. and Becher, H. (1972) *Atlas der Anatomie des Menschen. Band I: Regionen, Knochen, Bänder, Gelenke und Muskeln des menschlichen Körpers.* Urban & Schwarzenberg, München.
- Tax, A. A. M., Denier van der Gon, J. J. and Erkelens, C. J. (1990b) Differences in coordination of elbow flexor muscles in force tasks and in movement tasks. *Exp. Brain Res.* **81**, 567–572.
- Tax, A. A. M., Denier van der Gon, J. J., Gielen, C. C. A. M. and Kleyne, M. (1990a) Differences in central control of m. biceps brachii in movement tasks and force tasks. *Exp. Brain Res.* **79**, 138–142.
- Tax, A., Denier van der Gon, J. J., Gielen, C. C. A. M. and van den Tempel, C. M. M. (1989) Differences in the activation of m. biceps brachii in the control of slow isotonic movements and isometric contractions. *Exp. Brain Res.* **76**, 55–63.
- Theeuwen, M., Gielen, C. C. A. M. and Miller, L. E. (1994a) The relative activation of muscles during isometric contractions and low-velocity movements against a load. *Exp. Brain Res.* **101**, 493–505.
- Theeuwen, M., Gielen, C. C. A. M., Miller, L. E. and Doorenbosch, C. (1994b) The relation between surface EMG and recruitment thresholds of motor units in human arm muscles during isometric contractions. *Exp. Brain Res.* **98**, 488–500.
- Yeo, B. P. (1976) Investigations concerning the principle of minimal total muscular force. *J. Biomechanics* **9**, 413–416.
- Woittiez, R. D., Huijing, P. A., Boom, H. B. K. and Rozendal, R. H. (1984) A three-dimensional muscle model: a quantified relation between form and function of skeletal muscles. *J. Morphol.* **182**, 95–113.
- Zajac, F. E., Wicke, R. W. and Levine, W. S. (1984) Dependence of jumping performance on muscle properties when humans use only calf muscles for propulsion. *J. Biomechanics* **17**, 513–523.
- van Zuylen, E. J., Gielen, C. C. A. M. and Denier van der Gon, J. J. (1988) Coordination and inhomogeneous activation of human arm muscles during isometric torques. *J. Neurophysiol.* **60**, 1523–1548.